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Local and global stereopsis in the horse

Brian Timney *, Kathy Keil

Department of Psychology, Faculty of Social Science, Deans Office, University of Western Ontario, London, Ontario N6A 5C2, Canada

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Abstract

Although horses have laterally-placed eyes, there is substantial binocular overlap, allowing for the possibility that these animals have stereopsis. In the first experiment of the present study we measured local stereopsis by obtaining monocular and binocular depth thresholds for real depth stimuli. On all measures, the horses' binocular performance was superior to their monocular. When depth thresholds were obtained, binocular thresholds were several times superior to those obtained monocularly, suggesting that the animals could use stereoscopic information when it was available. The binocular thresholds averaged about 15 min arc. In the second experiment we obtained evidence for the presence of global stereopsis by testing the animals' ability to discriminate between random-dot stereograms with and without consistent disparity information. When presented with such stimuli they showed a strong preference for the cyclopean equivalent of the positive stimulus with the real depth. These results provide the first behavioural demonstration of a full range of stereoscopic skills in a lateral-eyed mammal.

Keywords: Depth; Horse; Stereoacuity; Stereopsis; Threshold

1. Introduction

It has been argued (Walls, 1942; Fox, 1978) that the evolutionary pressure favouring the frontal placement of the eyes in many species was, at least in part, driven by the requirements of binocular vision. By implication, animals with laterally-placed eyes and extensive monocular visual fields were not expected to have good stereopsis. Such animals were considered to rely predominantly on monocular cues for judging distance. Hughes (1977), however, has made a convincing case for the existence of stereopsis in lateral-eyed animals, pointing out the physiological data showing the presence of binocular neurons in the cortices of squirrel (Hall, Kaas, Killackey & Diamond, 1971), rabbit (Hughes, 1971), sheep (Clarke, Donaldson & Whitteridge, 1976) and goat (Clarke et al., 1976). Binocular neurons have also been reported in guinea pig (Choudhury, 1978) and hamster (Tiao & Blakemore, 1976). In sheep, goat and rabbit disparity-selective neurons have also been described (Van Sluyters & Stewart, 1974; Clarke et al., 1976).

In contrast to the wealth of suggestive physiological data, there are few behavioural studies of stereoscopic vision in lateral-eyed animals. Fox, Lehmkuhle and Bush (1977), and McFadden (1987) have obtained evidence for stereopsis in the falcon and pigeon, respectively, but we are unaware of any behavioural data on lateral-eyed mammals. Van Hof and Steele (1977) have shown that rabbits are able to learn tasks that require binocular integration, but they did not attempt to test for the presence of stereopsis. In the present study we provide evidence for both local and global stereopsis in a highly visual, lateral-eyed animal, the horse.

The horse provides an excellent model for the study of lateral-eyed stereopsis. Although its eyes are positioned to the sides of the head, with the optic axes diverging by approximately 40°, it also has as much as 65° of binocular overlap (Duke-Elder, 1958). In addition, the very large interpupillary separation found in this animal means that the angular disparity for a given distance from the fixation plane is much greater than that for smaller animals. Among humans, the introduction of an increased interocular distance through the use of a telesteresoscope provides an enhanced sensation of depth by increasing the relative disparity of the

* Corresponding author. Tel.: +1-519-661-2053; fax: +1-519-661-3868; e-mail: timney@julian.uwo.ca.

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retinal images (Wallach, Moore & Davidson, 1963). However, it remains to be demonstrated whether there is any relationship between large interocular distance and enhanced depth thresholds.

In the present study we tested for the presence of stereopsis in two ways. First, we measured monocular and binocular depth thresholds using real depth stimuli. The rationale for this kind of test is that of the Howard–Dolman apparatus (Howard, 1919). Briefly, we make the assumption that when the animal is viewing with one eye, there are monocular depth cues available that could allow it to perform the task. We have already shown that horses do seem to be able to make use of such cues (Timney & Keil, 1996). When they are allowed to use both eyes, these same monocular cues remain, but additional binocular cues, including retinal disparity, become available. If their binocular discrimination thresholds are better than their monocular, then we may assume that they are using the additional binocular cues and make the inference that they possess stereopsis. We have already shown in both the cat and meerkat that there are typically large differences between monocular and binocular thresholds (Mitchell, Kaye & Timney, 1979; Moran, Timney, Sorenson & Desrochers, 1983). It should be noted, however, that although this is a reasonable inference, it is not a definitive test of stereopsis. To provide stronger evidence, we conducted additional tests for the presence of global stereopsis using random-dot stereograms in which the only available cues are those provided binocularly.

2. Method

2.1. Experiment 1

2.1.1. Subjects

Two horses were used; the first (H1) was a 15 year-old thoroughbred mare, the second (H2) a 7 year-old Hanoverian/thoroughbred mare, both of whom had been used in previous psychophysical studies (Timney & Keil, 1992, 1996). They were stabled at a local farm and had free access to grazing pasture during the day. Both animals were ridden on a regular basis. Routine ophthalmic examinations showed clear ocular media.

2.1.2. Apparatus

The apparatus was identical to that used in a previous study, with the exception of the stimulus displays (Timney & Keil, 1996). Briefly, it consisted of a large wooden panel painted black and mounted on a stand with two trapdoors (41×51 cm) whose inner edges were located 19 cm to each side of the midline. The trapdoors had counterweights that allowed them to swing back easily and they were held closed by magnetic catches. Each could be locked when necessary. A small food pellet could be placed on a tray directly behind the door and this served as a reward in all the experiments. A 15 cm square aperture was cut into the centre of each trapdoor. The excised pieces were then mounted onto a rod that was held in place in the aperture in such a way that the now movable central square could be moved in 1 cm steps from 0 to 20 cm in front of the trapdoor. During initial training (see below) wooden dividers of varying lengths were placed midway between the trapdoors to prevent the animals from switching their choices once they had reached the trapdoors. Once criterion performance had been reached for the initial discriminations, a 2 m divider was used to set the minimum distance from which the animal could make a choice. Two full spectrum fluorescent light tubes placed above and in front of the apparatus illuminated the stimuli at an illuminance of approximately 1000 lx.

2.1.3. Stimuli

The test stimuli were mounted directly on to the trapdoors. They consisted of Plexiglas sheets painted matte white with black circles varying in diameter from 1.5 to 3 cm pasted randomly over the surface, including the central cut-out region.

2.1.4. Procedure

2.1.4.1. Preliminary training. All testing was conducted in an open area in the home stable where the animals could be led around from the apparatus to the starting point about 5 m away. They were tested in daily sessions by two experimenters. One experimenter led the animal towards the divider then released it allow it to make its decision. The other stood behind the apparatus and was responsible for changing the stimuli, recording the data and replenishing the food tray.

The horses were trained initially to approach the apparatus and to press their noses against one of the trapdoors to obtain the food pellet. The trapdoor containing the positive stimulus was switched according to a quasi-random sequence with the constraint that there were no more than three consecutive trials on one side. Once they had mastered this task, which they did very quickly, the training sessions were begun. There were three sets of training stimuli, as shown in Fig. 1. In all cases the positive stimulus was the dotted Plexiglas sheet with the central square set flush with the background. The decision to make the flat surface the positive stimulus was a pragmatic one because it made the task of pushing against the panel easier for the animals. For the first training series the negative stimulus was simply a black screen. For the second, the dotted central square was made to protrude from the black background by 20 cm, and for the third, the flat

dotted surface was paired with a full dotted screen with a protruding centre. The latter was the stimulus arrangement used in the rest of the study. For the training stimuli the animals were given between 30 and 40 trials per day until they had reached a criterion performance of 27 correct out of 30 consecutive trials. They were then moved on to the next set of stimuli.

After they had reached criterion on all of the training tasks, their depth discrimination thresholds were determined psychophysically. This was done in two stages. To obtain an initial estimate of threshold we used a modified method of limits. Trials were run in blocks of five, beginning with a negative stimulus containing a square that protruded markedly from the background. If the horse achieved four or five correct, the square was moved back by at least 2 cm for the next set of trials. If only three were correct, the depth separation was kept the same, and if less than three trials were correct it was increased. This procedure was continued until the animal had failed to make criterion at the smallest difference at least twice. Overall performance

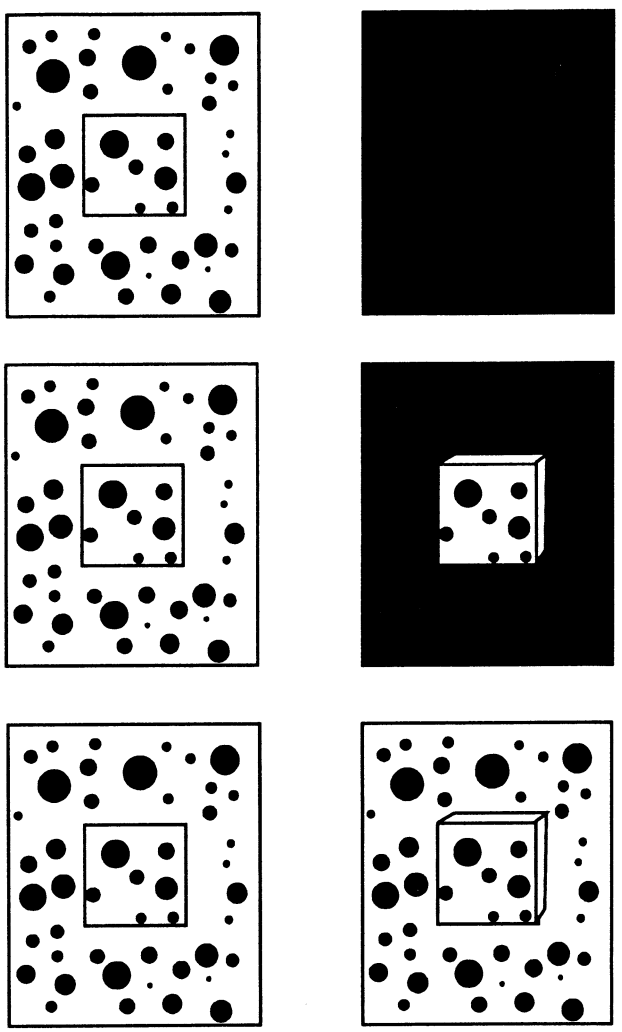

Fig. 1. Schematic representation of the three sets of training stimuli.

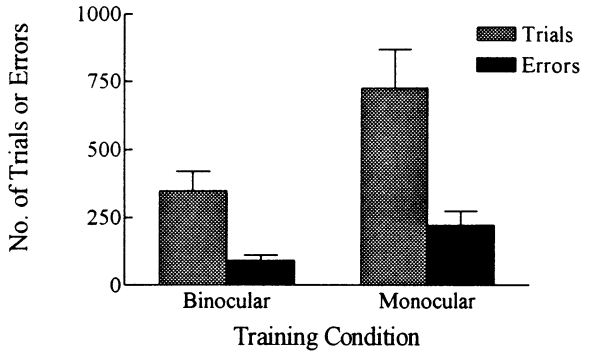

Fig. 2. Average number of trials and errors for the two horses for the third training task (protruding dotted surface on dotted background).

was cumulated over sessions and thresholds were taken as the smallest separation that the horse could discriminate on 70% of the trials. The use of a criterion of 70% made these data comparable with those gathered previously for the cat (cf. Mitchell et al., 1979). After a threshold estimate was obtained using the above procedure, the animals were run again using a method of constant stimuli. Five different depth separations were chosen to bracket the previous estimate. For each block of trials in a session one of these separations was chosen at random and presented five times. Then another separation was selected for the next block. This was continued until the horses had received ten trials at each of the five separations. Testing was continued until they had accumulated a total of at least 50 trials for each depth separation.

For both animals, all of the initial training and testing was carried out binocularly. Once the binocular thresholds had been obtained, they were retrained monocularly. This was achieved by requiring them to wear a mask containing an opaque eye cup that could be mounted over either eye using velcro fasteners.

2.1.5. Results

Overall, the two horses required 22 and 17 sessions and 850 and 655 trials, respectively to reach criterion on the three initial binocular training tasks. For the final discrimination, using the flat versus the protruding dotted surfaces they required an average of 348 trials. Once they had learned the task, however, they performed well during the threshold testing phase. However, when they were reintroduced to the task using one eye, their performance declined dramatically. As shown in Fig. 2, both animals required more trials to acquire the depth discrimination monocularly (an average of 724 trials) than they had using both eyes, despite having completed many hundreds of binocular trials during both training and subsequent threshold testing. For comparison purposes, the binocular data shown in the figure represents performance for the final discrimination task.

Their difficulty making monocular depth judgements was also evident in the measurements of depth discrimination thresholds. These data are presented in Fig. 3. They are expressed as percentage correct plotted as a function of the nominal angular retinal disparity. This value was calculated by taking as the viewing distance the closest point at which they could make a decision to go to one of the targets, the amount of protrusion of the central square, and the measured interpupillary distance. Obviously, a measure of disparity cannot be applied in the monocular case, so, to provide a common unit of measurement, the monocular thresholds were calculated as the amount of disparity that would have been present if both eyes were open. Both animals had much better binocular than monocular thresholds. The final values obtained, expressed in angular units of retinal disparity, were 10.7 and 18.7 min arc, respectively, while the monocular thresholds were 83.0 and 40.8 min arc, respectively. It is also worth noting the quite large differences in the monocular thresholds. Such variability in monocular thresholds is not uncommon, at least in cats (Timney, 1990) and may reflect a differential ability to take advantage of monocular depth cues.

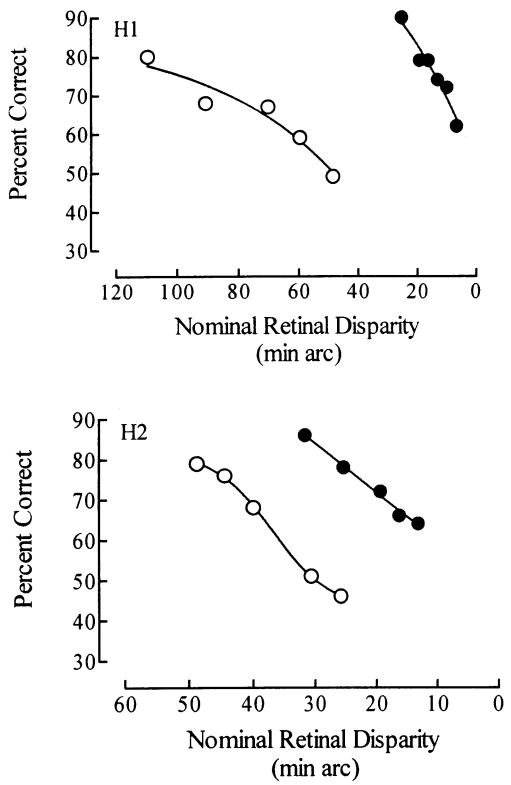

Fig. 3. Performance on the real depth task plotted as a function of the retinal disparity that would be present when viewing the targets from 2 m. Threshold was interpolated as the point at which performance fell to 70% correct. Filled circles: binocular; open circles: monocular.

3. Experiment 2

The comparison of monocular and binocular thresholds, while it provides strong presumptive evidence for the presence of stereopsis, is not definitive. The conclusion that stereopsis is present is based on the assumption that under both monocular and binocular viewing conditions, there are a number of monocular depth cues present. However, when both eyes are open the binocular cue of retinal disparity becomes available and any improvement in performance may be attributed to the use of this cue. Although it could be argued that the animals were simply disoriented by having one eye covered, there was nothing about their behaviour that suggested that this was the case. In addition, when the task was made very easy monocularly by having a large separation and allowing the animals to make their decision from a short distance, they had little difficulty with the task.

To establish definitively that the horse possesses stereopsis, a more stringent test is required. Furthermore, in the context of the question asked at the beginning of this paper, it is of interest to determine whether a lateral-eyed animal such as the horse might possess what is considered to be the most sophisticated form of binocular vision, global stereopsis (Julesz, 1971). We tested for this capacity in our horses using random dot stereograms.

3.1. Methods

3.1.1. Subjects

The same two animals were tested and the study was run several months after the measurement of real depth thresholds.

3.1.2. Apparatus and stimuli

The apparatus was identical with that of the first experiment; only the stimuli differed. The stimuli consisted of photographic reproductions of anaglyphic random dot stereograms taken from Julesz stereopsis testing patterns (Julesz, 1971). Two patterns were used, one with 100% correlated elements, which appeared to a human observer as a raised square in the centre of the field. The other contained only 40% correlated elements and no depth could be discerned. These stereograms were mounted on cards that could be displayed on the trapdoors. At a viewing distance of 200 cm, based on an interpupillary distance of 20 cm, the stereograms had a disparity of approximately 19 min arc. This corresponded to a real separation in depth of 12 cm. The horses wore the same face mask as before, but this time with transparent eye cups containing a red filter over one eye and a green filter over the other. For humans, these filters allowed the depth to be seen readily in the 100% correlated stereogram.

3.1.3. Procedure

The horses were initially retrained on the real depth discrimination of the previous experiment. Once they had achieved criterion, they were introduced to the filters and training was continued to ensure that they could maintain criterion performance while wearing them. Once a high level of performance was achieved, the testing began with the random dot stereograms. Trials with the stereograms were randomly interspersed with trials using real depth targets. The 40% correlated stereogram was designated as the 'positive' stimulus, although on these critical trials the animals were rewarded for approaching either of the two stimuli. A total of 35 critical trials were run.

After this phase of the experiment a series of control sessions was run to ensure that the horses were not making their discrimination based on potential non-relevant cues. For this part of the study, the animals were first given additional training with the random dot stereograms in which they were rewarded for going to the 'flat' side. Once they had achieved criterion, they were tested on alternate blocks of 20 trials with the standard random dot stereograms and either one, two 'flat' stereograms; two, the standard stereogram viewed with a green filter over each eye; three, the standard stereogram viewed with a red filter over each eye; and four, two stereograms, both of which contained depth. In those blocks of trials on which there should have been no basis for a discrimination, one of the stimuli was designated as 'correct' and the animal was rewarded for going to it. In each daily session they were run for 20 trials for each of the standard and control conditions.

3.2. Results

The results of the first part of this experiment are shown in the upper panel of Fig. 4. This shows that both horses approached the 'correct' stimulus, that is the one that appeared flat to a human observer, on almost 90% of the trials. They did this with no additional training and no differential rewards. The results of the control sessions are shown in the lower panel. For each of the control conditions, both horses were responding about equally to the two stimuli, while they continued to perform well for the standard stereogram. These data suggest very strongly that the horses were using the apparent depth in the random dot stereograms as cues and therefore we may conclude that they possess global stereopsis.

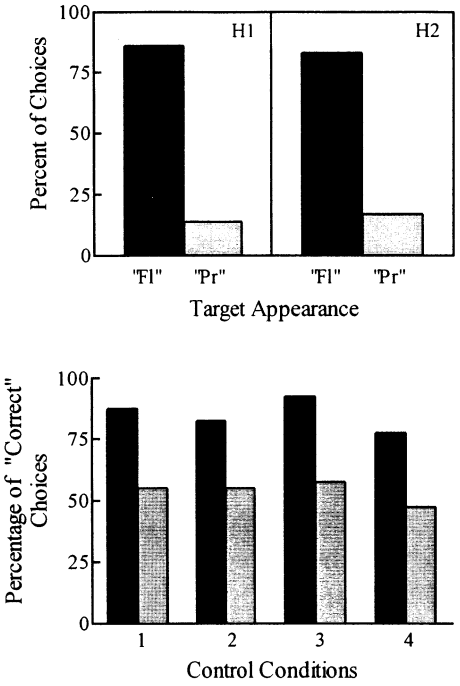

Fig. 4. Upper panel: percentage of choices to the 'flat' (Fl) and 'protruding' (Pr) random dot stereograms when the horses were rewarded for going to either target. Lower panel: performance on each of the control conditions. (1) Both targets 'flat'; (2) both eyes covered with a green filter; (3) both eyes covered with a red filter; (4) both targets 'protruding'. Black bars indicate the percentage of correct choices to the standard pair of stereograms, stippled bars show the percentage of choices to one of the control pair targets that was arbitrarily designated as 'correct'.

4. Discussion

The clear superiority of binocular performance in the first experiment suggests very strongly that horses possess at least local stereopsis. In comparison to other non-primate species, the obtained thresholds at first appear rather poor. For example, the best values obtained for cats using similar testing procedures are in the order of 2–4 min (Mitchell et al., 1979) and 1–2 min in the pigeon (McFadden, 1987). However, if we consider the data in terms of the amount of depth separation that these animals can detect, a different picture emerges. The horse has a very large interpupillary distance, about 20 cm in the average animal. This may be contrasted with the 3.5 cm of the cat and about 2.4 cm in the pigeon. Because retinal disparity varies directly with interpupillary distance, the effect of increasing it is to generate a larger disparity for any given separation in depth between two targets. Thus, the average binocular threshold for the two horses was 14.8 min arc. This is equivalent to a separation of 9 cm when viewed from a distance of 2 m. If we calculate the angular value for this depth separation in the cat and the pigeon using their smaller interpupillary distances, we obtain values of 2.6 and 1.8 min arc, respectively, values that are fairly close to the measured disparity thresholds for these species. It appears then, that in terms of absolute distance thresholds, the horse performs as well as the cat and pigeon. This result suggests

that the larger angular disparity provided by the large interocular separation does not necessarily confer an advantage in making fine depth judgements. It is possible that the larger interocular distance provides for appropriate depth judgements within the normal 'working distance' of the animal. For example, the pigeon, with closely spaced eyes, forages for food at distances of only a few centimetres, whereas the horse, in moving about its environment must make judgements over a range of several meters.

In computing retinal disparity above we used the conventional formulae for frontal-eyed animals (Mitchell et al., 1979). However, for lateral-eyed species the processing of stereoscopic depth information poses somewhat different problems from those of animals with frontal eyes. Although overlap of the optical visual fields is essential, it is also necessary to take into account the locus of binocular overlap in retinal coordinates. Holden and Low (1989) have pointed out, that for animals with divergent optical axes, binocular vision is subserved only by disparate retinal points. If the eyes cannot not be brought into convergent register, the fixation point will fall in the temporal retina of each eye. Although an anatomically defined reference point is not necessary for the computation of retinal disparity, it is of interest to raise the question of how stereoscopic depth information might be coded in lateral-eyed animals.

Although horses certainly have the ability to move their eyes, there is no information on whether they have an effective vergence system. If their vergence is limited then, in principle, they could code absolute distance by comparing the positions of the images in the two eyes (cf. Collett & Harkness, 1982). The very large interocular separation in horses could make this an effective cue. However, nothing is known about receptive field disparities in the equine eye so it is uncertain whether they could use such a mechanism.

An alternative mechanism that assumes some vergence ability has been suggested by Choudhury (1980), working with the rabbit. He found clusters of binocularly responsive units in which the location of the receptive fields in the ipsilateral eye tended to shift temporally with respect to those in the contralateral eye along the course of an electrode penetration. He proposed a model to account for these data, suggesting that the locus of the reference corresponding point could vary with amount of vergence. In effect, the amount of disparity signalled by a particular locus on the retina would vary with fixation distance.

As mentioned above, the use of random dot stereograms provides a more rigourous test of stereopsis than the use of real depth stimuli. In the present study, with no prior exposure to such patterns and no differential reward, the horse showed an almost exclusive preference for the 'flat' surface that corresponded to the positive stimulus in the real depth conditions. This result may be taken as strong evidence for the presence of global stereopsis in horses. In the control conditions, the animals' performance fell to chance when no differential depth information was present in the stimuli, further supporting that conclusion. However, it could be argued that the validity of the control conditions is questionable because the training trials given with the random dot stereograms may have allowed the horses to learn the discrimination on the basis of idiosyncratic dot clusters in the stimuli. While we can not rule out this possibility entirely, it seems highly unlikely. The strongest evidence against the argument is the fact that the animals showed a strong initial preference for the 'correct' stimulus with no prior exposure. During the subsequent training sessions it seems reasonable to assume that they were using the same information that they had used on the initial critical trials as the basis for making their discrimination, rather than seeking the much less obvious cue of dot clustering. Close inspection of the stimuli did not reveal any obvious clustering of the dots in the patterns, at least to humans. Thus, we would argue that the differential performance under the control conditions should be taken as further evidence that the animals were able to make discriminations based on the depth information present in the stereograms.

Several years ago (Fox, 1978) described two hypotheses concerning the evolution of binocular vision and stereopsis. The 'elitist' hypothesis proposed that the mechanisms of stereopsis were associated with the emergence of mammals and reached their culmination in primates. The 'proletarian' hypothesis suggests that stereopsis may be present in all animals with binocular vision. It is now clear from recent evidence that stereopsis is by no means restricted to mammals, but is present in some form at many levels in the phylogenetic scale (Bough, 1970; Collett, 1977; Fox & Blake, 1971; Fox et al., 1977; Martinoya, Houezec & Bloch, 1988; Rossel, 1983). The results of the two experiments described above provide evidence that among mammals, stereopsis is not confined to species with frontal eyes. In addition, and perhaps of greater significance, is the finding that global stereopsis may also be found in lateral-eyed animals. It is evident that the complex computational mechanisms required for the extraction of information from random-dot stereograms are available across many different species, suggesting that this capacity is a rather fundamental aspect of binocular vision and that a strong form of the 'proletarian' hypothesis described by (Fox, 1978) is appropriate.

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